Main prey and predators of Atlantic mackerel (*Scomber scombrus* L.) in the northern and southern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s

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Main prey and predators of Atlantic mackerel (*Scomber scombrus* L.) in the northern and southern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s

by

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ABSTRACT

Savenkoff, C., F. Grégoire, M. Castonguay, D.P. Swain, D. Chabot, and J.M. Hanson. 2005. Main prey and predators of Atlantic mackerel (*Scomber scombrus* L.) in the northern and southern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2619: v+29 pp.

We used results of mass-balance models to describe the changes in the structure and functioning of the northern and southern Gulf of St. Lawrence ecosystems related to the Atlantic mackerel (*Scomber scombrus* L.) stock for the mid-1980s, the mid-1990s, and the early 2000s. The net decrease in biomass of demersal species and the ensuing drop in predation from the mid-1980s to the mid-1990s led to an ecosystem structure dominated by small-bodied pelagic species and marine mammals in the northern and southern Gulf. Predation was the main cause of mackerel mortality in each ecosystem for all time periods. However, demersal predators such as large cod and large demersals were progressively replaced by cetacea and seals as the main mackerel predators from the mid-1980s to mid-1990s (and early 2000s in the northern Gulf). Over the same time period, fishing mortality increased and became the second highest mortality cause in the northern Gulf for the early 2000s and the main mortality cause in the southern Gulf for the mid-1990s. Fishing mortality may have been underestimated due to non-negligible under-reporting (discards at sea, recreational catches, and catches by bait fishermen).

RÉSUMÉ

Savenkoff, C., F. Grégoire, M. Castonguay, D.P. Swain, D. Chabot, and J.M. Hanson. 2005. Main prey and predators of Atlantic mackerel (*Scomber scombrus* L.) in the northern and southern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2619: v+29 pp.

Nous avons utilisé les résultats de modèles d'équilibre de masse pour décrire les changements dans la structure et le fonctionnement des écosystèmes du nord et du sud du golfe du Saint-Laurent associés au stock de maquereau de l'Atlantique (*Scomber scombrus* L.) pour le milieu des années 1980, le milieu des années 1990 et le début des années 2000. La forte diminution des biomasses des espèces démersales et la chute résultante de la pression de prédation qu'elles exercent depuis le milieu des années 1980 jusqu'au milieu des années 1990 ont conduit à une structure de l'écosystème dominée par des petits poissons pélagiques et des mammifères marins dans le nord et le sud du Golfe. La prédation était la principale cause de mortalité du maquereau dans chaque écosystème et à chaque période. Cependant les prédateurs démersaux tels que la morue et les grands démersaux ont été progressivement remplacés par les cétacés et les phoques comme principaux prédateurs du maquereau depuis le milieu des années 1980 jusqu'au milieu des années 1990 (et le début des années 2000 pour le nord du Golfe). Durant la même période de temps, la mortalité par pêche a augmenté et est devenue la seconde cause de mortalité dans le nord du Golfe au début des années 2000 et la principale cause de mortalité dans le sud du Golfe pour le milieu des années 1990s. La mortalité par pêche a pu être sous-estimée à cause de captures non déclarées qui seraient non négligeables (rejets en mer, captures récréatives et captures réalisées par les pêcheurs d'appât).

INTRODUCTION

In the early 1990s, the abundance of many Northwest Atlantic cod (*Gadus morhua*) populations declined to low levels, resulting in the cessation of directed fishing for these stocks (CAFSAC 1994). Mass-balance models using inverse methodology have been constructed for the northern Gulf of St. Lawrence (Savenkoff et al. 2004a; Savenkoff et al. submitted a[1]) and for the southern Gulf of St. Lawrence (Savenkoff et al. submitted b[2]) before and after the collapse of groundfish stocks (hereafter termed mid-1980s and mid-1990s, respectively) and in the early 2000s, at the end of the moratorium on cod fishing, for the northern Gulf only. The results highlight the effects of major mortality causes (fishing, predation, and other mortality) on the fish and invertebrate communities and major changes in the structure and function of the northern and southern Gulf ecosystems over the last two decades.

Overfishing removed a functional group, large piscivorous fish, which has not been replaced ten years after the cessation of heavy fishing. This has left only marine mammals as top predators during the mid-1990s, although small Greenland halibut (*Reinhardtius hippoglossoides*) became important predators in the northern Gulf during the early 2000s. Overfishing during the 1980s appears to have thus caused a regime shift in the northern and southern Gulf ecosystems over the past two decades. The net decrease in biomass of the demersal species and the ensuing drop in predation from the mid-1980s to the mid-1990s led to ecosystem structures dominated by small-bodied pelagic species and marine mammals in the northern and southern Gulf (Savenkoff et al. submitted a, b). These changes were accompanied by a decrease in total catches and a transition in landings from long-lived, piscivorous groundfish toward planktivorous pelagic fish and invertebrates in agreement with the fishing down of marine food webs reported by Pauly et al. (1998) for the Northern Hemisphere.

Shifts from ecosystems dominated by demersal fish to ecosystems dominated by pelagic fish (or short-lived species such as shrimp, crabs, or octopus) have been documented in the Atlantic and the Baltic (Worm and Myers 2003, Frank et al. 2005) and other coastal ecosystems (Jackson et al. 2001). Large piscivorous predators declined dramatically, but their prey (e.g., forage species such as herring, capelin, shrimp, and snow crab) increased in abundance (Lilly 1991, Berenboim et al. 2000, Garrison and Link 2000, Koeller 2000, Lilly et al. 2000). With capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus* L.) make up a large pelagic forage base that supported the high level of predation in the Gulf of St. Lawrence (i.e., mid-1980s; Savenkoff et al. 2004a). Based on the results of mass-balance models, we present in this report the changes in the structure and functioning of the Gulf ecosystems for the mid-1980s, the mid-1990s, and the early 2000s as they relate to the Atlantic mackerel stock. Our results enabled us to evaluate the main prey and predators of mackerel as well as the effects of fishing and predation on this species for each ecosystem and each time period. There is only one mackerel population in eastern Canada, with variable proportions of the population occupying the northern and southern Gulf of St. Lawrence from June to November.

[1]submitted a: Savenkoff, C., Castonguay, M., Chabot, D., Bourdages, H., Morissette, L., and Hammill, M. O. Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? Submitted for publication.

[2]submitted b: Savenkoff, C., Swain, D. P., Hanson, J. M., Castonguay, M., Hammill, M. O., Bourdages, H., Morissette, L., and Chabot, D. Effects of fishing and predation in a heavily exploited ecosystem: Comparing pre- and post-groundfish collapse periods in the southern Gulf of St. Lawrence (Canada). Submitted for publication.

MATERIAL AND METHODS

Data used in modelling

The study area (depths > 37 m) in the northern Gulf of St. Lawrence (Northwest Atlantic Fishing Organization [NAFO] divisions 4RS) covers 103,812 km^2 (Figure 1). In the southern Gulf (NAFO division 4T), the study covers a 64,075 km^2 area between the depths of 15 m and 200 m and excludes the deep parts of the Laurentian Channel and the estuary (Figure 1). Infra-littoral species and American lobster (*Homarus americanus*) were not included in the models. This zone was excluded from the models because exchanges between the infra-littoral and pelagic zones are still poorly understood. The periods covered by this analysis are the pre-collapse (mid-1980s: 1985–1987) and post-collapse (mid-1990s: 1994–1996) periods of groundfish stocks in both areas. For the northern Gulf, another period was also studied: the early 2000s (2000-2002), a few years after a limited cod fishery had resumed in the northern Gulf.

Based on data availability and the ecological and commercial significance of the species, the whole-system model of the northern Gulf of St. Lawrence was divided into different functional groups or compartments (32 for the mid-1980s and mid-1990s, 31 for the early 2000s) representing the main pelagic, demersal, and benthic species present (Table 1). The model structure for the early 2000s differs slightly from that used for the mid-1980s and mid-1990s for the following reasons: (1) improved knowledge: cetaceans were separated into mysticeti (baleen whales) and odontoceti (toothed whales); (2) newly available data on biomass of size classes for shrimp and crabs that allowed separating these species into small and large groups for the early 2000s; (3) very low biomass for the early 2000s: sand lance *Ammodytes* spp. (biomass: 0.003 t km^{-2} vs 2.398 and 0.120 t km^{-2} for the mid-1980s and mid-1990s, respectively) were included in the planktivorous small pelagic feeders group for the early 2000s; (4) a combination of limited data and a weak trophic role in the mid-1980s and mid-1990s ecosystems for hooded seals (*Cystophora cristata*), harbour seals (*Phoca vitulina*), and Arctic cod (*Boreogadus saida*) resulted in these groups being combined with the harp seal (*Pagophilus groenlandica*), grey seal (*Halichoerus grypus*), and capelin (*Mallotus villosus*) groups, respectively, for the early 2000s. For the mid-1980s and mid-1990s, we distinguished five marine mammal groups, one seabird group, sixteen fish groups, eight invertebrate groups, one phytoplankton group, and one detritus group (Table 1). For the early 2000s, we distinguished four marine mammal groups, one seabird group, fourteen fish groups, ten invertebrate groups, one phytoplankton group, and one detritus group (Table 1). Shrimp and crabs were each separated into two groups. Based on an average size at sex change (22 mm carapace length, CL), shrimp were separated into large shrimp (≥ 22 mm CL), mainly female *Pandalus borealis*, which are recruited to the fishery, and small shrimp (< 22 mm CL), mainly male *P. borealis* and individuals from other shrimp species, which are not recruited to the fishery (DFO 2002). Based on important differences in diet, vulnerability to predation (in particular cannibalism; crab prey ranged between 3.9 and 48.8 mm carapace width, CW), and minimal carapace width of adult snow crabs (40 mm CW), crabs were separated into small (≤ 45 mm CW) and large (> 45 mm CW) crabs (Lovrich and Sainte-Marie 1997). Only large crabs are recruited to the fishery and consist almost exclusively of male snow crab, *Chionoecetes opilio*.

In the southern Gulf of St. Lawrence, we distinguished 30 functional groups consisting of five marine mammal groups, one seabird group, fourteen fish groups, eight invertebrate groups,

one phytoplankton group, and one detritus group for the mid-1980s and mid-1990s (Table 1). No model has been constructed for the early 2000s.

In both ecosystems, some groups, such as large pelagic and demersal feeders, are composite groups, where the species were aggregated based on similarity in size and ecological role. Atlantic cod, Greenland halibut (*Reinhardtius hippoglossoides*) (in the northern Gulf), and American plaice (*Hippoglossoides platessoides*) (in the southern Gulf) were, for some models, separated into two groups based on diet, age/size at first capture, and age/size at maturity. Juveniles of these species prey mainly on invertebrates while larger individuals feed mostly on fish. These changes tend to occur gradually with increasing length, but for these models it was assumed that the change occurs at 35 cm for cod (Lilly 1991) and American plaice (Pitt 1973) and at 40 cm for Greenland halibut (Bowering and Lilly 1992). Due to a lack of length-frequency data and information on diet compositions of small versus large fish as well as on the proportions of juvenile and adult fish in the diets of their predators, we could not distinguish juveniles and adults for other fish species.

To estimate the magnitude of trophic fluxes, the models require measurements or estimates of different parameters (input data) such as biomass, diet composition, and landings as well as consumption and production rates for different living compartments. For the northern Gulf, diet composition and the other input data (biomass, production, consumption, and export) for each compartment as well as calculation details are described in Morissette et al. (2003) for the mid-1980s, Savenkoff et al. (2004b) for the mid-1990s, and Savenkoff et al. (2005) for the early 2000s. For the southern Gulf, further details on the calculation of diet composition and the other input data (biomass, production, consumption, and export) for each compartment are given in Savenkoff et al. (2004c). These technical reports are available online: www.osl.gc.ca/cdeena/en/publications.shtml.

Inverse modelling

Inverse models use mass-balance principles and an objective least-squares criterion to estimate flows of organic matter or energy among components of an ecosystem and to generate a "snapshot" of the system at one moment in time (Vézina and Platt 1988; Savenkoff et al. 2004a). As opposed to traditional approaches, the ecosystem is considered as a whole, taking into account trophic interactions between all functional groups. Inverse methods provide a powerful tool to estimate ecosystem flows using limited data and straightforward mass balance and metabolic constraints.

Under the steady-state assumption, consumption representing the input must balance the sum of the outputs consisting of production, respiration, and egestion (flux of unassimilated food: feces or detrital flow) for each group. In these models, we assumed steady state, i.e., no year-to-year change in biomass during each time period and zero net migration (migration out of or into the study area, food intake by predators that are not part of the system, etc.). Thus, production was equal to the biomass lost to fishing, predation, and natural mortality other than predation (hereafter termed other mortality causes or MO). Other mortality causes include other natural causes of death such as disease or could reflect unsuspected processes occurring in the ecosystem, such as misreported catch (e.g., Savenkoff et al. 2004a), unsuspected migration, or other processes not accounted for in the model. For phytoplankton, the net (corrected for respiration)

production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus were assumed to respire. Details of the model structure and method of solution for the different equations are given in Savenkoff et al. (2004a and submitted a, b).

The models are useful in constraining observations into coherent pictures (Savenkoff et al. 2004a and submitted a, b); however, since the number of flows to be solved exceeded the number of independent mass balance relations (i.e., an underdetermined system), there is no unique solution to any model. Also, it remains that the results are sensitive to some choices we made regarding the modelling structure and that other valid solutions are possible. However, for each model presented in the next section, the final solution is always the mean of 30 iterations with random perturbations of the input data (to a maximum of their standard deviations) and one solution without perturbation (the "initial solution") to provide an overall view of the ecosystem and to identify robust patterns. The estimated flows fell inside our *a priori* constraints and therefore were a reasonable "middle ground" description. Simulated inverse analyses have shown that the general flow structure of ecosystems can be recovered with these techniques, although the details can be inaccurate (Vézina and Pahlow 2003).

Background on mackerel

Mackerel populations in the Northwest Atlantic form a stock complex that overwinters off the New England coast. A part of this stock complex then migrates northwards in May and June to spawn in the southern Gulf of St. Lawrence (Sette 1950; Moores et al. 1975). The preferred temperatures range from 7.3°C to 15.8°C (Olla et al. 1976). Mackerel begin to spawn at 9-10°C, with maximum spawning occurring at 12°C (Sette 1950). After spawning, they disperse throughout the Gulf for the rest of the summer (DFO 2003).

Mackerel landings in the Northwest Atlantic (NAFO subareas 2-6) reached high values in the 1970s (between 300,000 t to 450,000 t). Landings then dropped considerably in 1977 with the introduction of the 200-nautical-mile economic exclusion zone (EEZ) (Figure 2). Owing to agreements between the United States and eastern European countries, landings increased again in the early 1980s, peaking at close to 85,000 t in 1988. In the ensuing years, landings dropped considerably as the United States gradually reduced its mackerel quotas to eventually completely close the foreign fishery in 1992. Since the early 2000s, catches have been increasing again due to an abundant year-class (1999) and a considerable increase in fishing effort on this species. Since 1987, Canada has been proposing that the total allowable catch (TAC) of 200,000 t for the entire Northwest Atlantic be divided equally with the United States. In light of the low biomass estimates derived from the 1996, 1998, and 2000 egg surveys, the Canadian share of the TAC was reduced from 100,000 t to 75,000 t in 2001 (DFO 2005). Of all mackerel catches reported in Canada in 2004, 32,966 t or 94% were landed in Newfoundland, i.e., 11,548 t in divisions 3K and 3L, and 21,418 t in division 4R (Table 2). The purse seine was the main fishing gear used, totaling 32,966 t, followed by gillnets and jiggers, totaling 1,196 t and 860 t, respectively (DFO 2005).

Input data (biomass, production, consumption, and catch) used in modelling and estimated fluxes for mackerel for each ecosystem and each period are summarized in Table 3. For 1985–1987 in the northern Gulf, we used the estimates of the model solution including misreported catches of large cod (Savenkoff et al. 2004a). In our models, the piscivorous small pelagic feeders group includes Atlantic mackerel, short-finned squid (*Illex illecebrosus*), and piscivorous juveniles of large pelagics. Atlantic mackerel was the most important in terms of biomass (99% of biomass) and was therefore considered the key species for the group. Some values were slightly different from data published in previous technical reports (Morissette et al. 2003, Savenkoff et al. 2004b-c, Savenkoff et al. 2005) due to model updates.

Catch

Commercial landings were estimated from NAFO landing statistics (NAFO 2003). In the northern Gulf, the mean annual total catch was 1,297 t or 0.01 t km^{-2} yr^{-1} (SD: 0.02 t km^{-2} yr^{-1}; range: 0.00-0.03 t km^{-2} yr^{-1}) during the 1985–1987 period, 3,060 t or 0.03 t km^{-2} yr^{-1} (SD: 0.01 t km^{-2} yr^{-1}; range: 0.02-0.04 t km^{-2} yr^{-1}) during the 1994–1996 period, and 7,078 t or 0.07 t km^{-2} yr^{-1} (SD: 0.05 t km^{-2} yr^{-1}; range: 0.02-0.11 t km^{-2} yr^{-1}) during the 2000–2002 period. The modelling catch estimate was 0.01, 0.03, and 0.07 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

In the southern Gulf, the landings of the piscivorous small pelagic feeders were also calculated by summing NAFO landing statistics for each of the species listed above (NAFO 2003). For Atlantic mackerel, the mean annual landings in 4T were 9,896 and 9,971 t during the 1985–1987 and 1994–1996 periods, respectively. Since the study area covered only a fraction of 4T (area between the depths of 15 and 200 m), a correction factor for catch was used. This correction factor, estimated using the biomass ratio between the study area and 4T, was 1.00 for the two periods. For short-finned squid, there were no landings in 4T during the 1985–1987 period while the mean annual landings were 28 t during the 1994–1996 period. The area correction factor was 0.63 during the mid-1990s. This resulted in mean annual catches of piscivorous small pelagics of 0.14 ± 0.04 and 0.14 ± 0.02 t km^{-2} yr^{-1} in the mid-1980s and mid-1990s, respectively. The modelling catch estimate of piscivorous small pelagics was 0.13 and 0.15 t km^{-2} yr^{-1}, respectively, for each of the two periods.

Biomass

In the northern Gulf, spawning stock estimates for mackerel were derived from an egg production index calculated for 1983 to 2002 for the southern Gulf of St. Lawrence (DFO 2003). These estimates are for the spawning stock only and will be underestimated if some mackerel spawn prior to entering the Gulf (DFO 2003) or outside of the period sampled by the research survey. No biomass estimates of juvenile mackerel were available. We did not apply a residence time factor to reduce biomass because mackerel feeds mainly during the summer period when they are in the Gulf. After spawning, mackerel disperse throughout the entire area (NAFO divisions 4RS and 4T). There is little information about the proportion of mackerel that moves into the northern (4RS) versus southern (4T) Gulf. Based on research vessel survey data and

expert opinion, we assumed that one third of the biomass moved into 4RS while the other two thirds were distributed in 4T.

Knowing that the northern Gulf represents 59.7% of the trawlable surface area of the entire Gulf of St. Lawrence, mackerel biomass was estimated to be 254,986 t or 2.46 t km^{-2} (SD: 0.85 t km^{-2}) for 1985–1987, 57,978 t or 0.56 t km^{-2} (SD: 0.45 t km^{-2}) for 1994–1996, and 90,680 t or 0.52 t km^{-2} (SD: 0.29 t km^{-2}) for 2000–2002.

In the southern Gulf, the mean biomass estimates were 316,089 t or 4.93 t km^{-2} (SD: 1.70 t km^{-2}) and 74,125 t or 1.16 t km^{-2} (SD: 0.90 t km^{-2}) for 1985–1987 and 1994–1996, respectively.

Production

Due to the lack of reliable information on production (P) and total mortality (Z) for mackerel in NAFO divisions 4RST, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch (Allen 1971). Natural mortality was set to 0.2 yr^{-1} in the absence of better information.

In the northern Gulf, when the minimum and maximum biomass values were used for each period, we obtained production ranges of 0.34 to 0.68 t km^{-2} yr^{-1} (mean: 0.48 ± 0.17 t km^{-2} yr^{-1}) for 1985–1987, 0.08 to 0.20 t km^{-2} yr^{-1} (mean: 0.14 ± 0.06 t km^{-2} yr^{-1}) for 1994–1996, and 0.08 to 0.25 t km^{-2} yr^{-1} (mean: 0.17 ± 0.12 t km^{-2} yr^{-1}) for 2000–2002. The modelling production estimate for mackerel was 0.64, 0.20, and 0.25 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

In the southern Gulf, when the minimum and maximum biomass values were used for each period, we obtained production ranges of 0.75 to 1.54 and 0.28 to 0.53 t km^{-2} yr^{-1}, respectively, for each period. The modelling estimates were 1.14 and 0.44 t km^{-2} yr^{-1} for 1994–1996 and 2000–2002, respectively.

Consumption

Information was gathered from two sources. Mehl and Westgard (1983) estimated mackerel consumption in the North Sea to be 6% of body mass per day (N = 3,674). A consumption/biomass (Q/B) ratio of 2.190 yr^{-1} was thus estimated from this information. Also, a Q/B value of 4.400 yr^{-1} for Atlantic mackerel was taken from FishBase (Froese and Pauly 2002).

In the northern Gulf, when the minimum and maximum biomass values and the different previous Q/B ratios were used for each period, we obtained a consumption range of 3.66 to 14.79 t km^{-2} yr^{-1} for 1985–1987, 0.53 to 3.85 t km^{-2} yr^{-1} for 1994–1996, and 0.70 to 3.21 t km^{-2} yr^{-1} for 2000–2002. Based on the mean production for each period and the minimum and maximum gross growth efficiency limits (GE; the ratio of production to consumption; 10–30%; Christensen and Pauly, 1992), we obtained consumption values of 1.60 and 4.81 t km^{-2} yr^{-1} for 1985–1987, 0.46 and 1.37 t km^{-2} yr^{-1} for 1994–1996, and 0.56 and 1.68 t km^{-2} yr^{-1} for 2000–2002. However, assuming that these species would eat at least as much food as their biomass per year ($Q/B \geq 1$), the resulting lower and upper consumption limits used were 2.46 and 14.79 t km^{-2} yr^{-1} for 1985–1987, 0.56 and 3.85 t km^{-2} yr^{-1} for 1994–1996, and 0.56 and 3.21 t km^{-2} yr^{-1} for 2000–2002. The

inverse solution estimated a consumption of 2.71 t km^{-2} yr^{-1} for 1985–1987, 0.93 t km^{-2} yr^{-1} for 1994–1996, and 1.09 t km^{-2} yr^{-1} for 2000–2002 in the northern Gulf.

In the southern Gulf, when the minimum and maximum biomass values for each period and the previous Q/B ratios were used, we obtained consumption ranges of 7.37 to 29.65 t km^{-2} yr^{-1} for 1985–1987 and 1.15 to 7.88 t km^{-2} yr^{-1} for 1994–1996. Based on the mean production (1.09 and 0.40 t km^{-2} yr^{-1}) for each period and the minimum and maximum GE limits (10–30%), we obtained other consumption ranges of 3.64 to 10.93 and 1.33 to 3.99 t km^{-2} yr^{-1} for 1985–1987 and 1994–1996, respectively. Assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), the resulting lower and upper consumption limits used were 4.93 to 29.65 t km^{-2} yr^{-1} and 1.16 to 7.88 t km^{-2} yr^{-1}, respectively, for the two periods. The inverse solution estimated a consumption of 8.01 and 3.36 t km^{-2} yr^{-1} for 1985–1987 and 1994–1996, respectively.

Diet composition

In the northern Gulf, diet composition inputs were derived from different sources of information on Atlantic mackerel, the key species for the piscivorous small pelagic group. On the Scotian Shelf, the main prey in 199 mackerel stomachs were hyperiid amphipods, euphausiids, and fish larvae (mainly blennoids and gadoids) (Kulka and Stobo 1981). The other diet study examined 359 stomachs of mackerel from the Gulf of St. Lawrence and the Scotian Shelf (Grégoire and Castonguay 1989). The main prey species (in % abundance) were found to be nematodes (which were probably stomach parasites), copepods, and unidentified larvae. The resulting diet composition for 1985–1987 is shown in Table 4. For 1994–1996, we also used the study of Darbyson et al. (2003) in the southern Gulf. In that study, the main prey in 265 mackerel stomachs were capelin, euphausiids, and copepods. The resulting diet composition is shown in Table 4. For 2000–2002, we also used the diet composition estimated by Savenkoff et al. (2004c) for the southern Gulf of St. Lawrence based on stomach content data for mackerel from June to September 1999 (n = 515). The resulting diet composition for 2000–2002 is shown in Table 4. At each period, we decided to use all the available diet compositions, even though they were from the southern Gulf.

In the southern Gulf, diet composition was derived from two sources of information on Atlantic mackerel, the key species for this group. Stomach content data for mackerel were available from NAFO division 4T from June to September 1999 (n = 515) (M. Hanson, unpublished data). We used these diet data for the two periods. However, for 1985–1987, we also used the diet composition estimated for the Gulf of St. Lawrence and the Scotian Shelf (n = 359) from Grégoire and Castonguay (1989). The resulting diet composition for each period is shown in Table 5.

RESULTS

Main prey groups consumed by mackerel

Small and large zooplankton were the main prey during the three periods in the northern Gulf (Figure 3). Small and large zooplankton accounted for 70 and 30%, respectively, of the diet during the mid-1980s while they contributed 42 and 47%, respectively, of the diet during the mid-1990s. During the early 2000s, small and large zooplankton accounted for 51 and 24%, respectively, of the diet. Large zooplankton are organisms and species greater than 5 mm in length and include euphausiids (mainly *Thysanoessa raschii*, *T. inermis*, and *Meganyctiphanes norvegica)*, chaetognaths (mainly *Sagitta elegans*), hyperiid amphipods (mainly *Themisto libellula*, *Parathemisto abyssorum*, and *P. gaudichaudii*), jellyfish (cnidarians and ctenophores), mysids (mainly *Boreomysis arctica*), tunicates, and ichthyoplankton. The small zooplankton includes zooplankton less than or equal to 5 mm in length. Copepods, mainly *Calanus finmarchicus* and *Oithona similis*, are the most numerous small zooplankton. In our inverse models, we were not able to estimate the individual proportion of each species aggregated in large and small zooplankton groups consumed by mackerel. A decrease in the mackerel consumption was estimated by the models from the mid-1980s to the mid-1990s (from 2.7 ± 1.6 to 0.9 ± 0.7 t km^{-2} yr^{-1}; Figure 3) in relation to the decrease in mackerel biomass (Table 3). During the early 2000s, the proportions of shrimp and other benthic invertebrates increased in the diet (4 and 5%, respectively, of the diet) while the proportion of capelin remained high (14%; Figure 3). The overall consumption of mackerel was similar to that for the mid-1990s (1.1 ± 0.8 t km^{-2} yr^{-1}; Figure 3).

In the southern Gulf, small and large zooplankton were the most important prey for the two periods (96 and 74%, respectively, of the diet for the two time periods) (Figure 4). During the mid-1990s, shrimp and capelin contributed nearly 10% each to the diet. A decrease in mackerel consumption was estimated by the models from the mid-1980s to the mid-1990s (from 8.0 ± 2.9 to 3.4 ± 2.3 t km^{-2} yr^{-1}; Figure 4) in relation to the decrease in mackerel biomass (Table 3).

Main vertebrate and crustacean prey consumed in the northern and southern Gulf ecosystems

In the northern Gulf, when planktonic and benthic invertebrate groups were not considered in the calculation, capelin was the major prey in the system and accounted for 57 and 63% of the matter consumed in the mid-1980s and the mid-1990s, respectively (Figure 5). The other main prey groups were planktivorous small pelagics (mainly Atlantic herring *Clupea harengus*), redfish (*Sebastes* spp.), and shrimp (mostly *Pandalus borealis*) during the mid-1980s. During the mid-1990s, shrimp and planktivorous small pelagics were heavily consumed in the ecosystem (Figure 5). There was a four-fold decrease in the matter consumed from the mid-1980s to mid-1990s (from 19.1 ± 3.0 to 4.8 ± 0.5 t km^{-2} yr^{-1}; Figure 5). From the mid-1990s to early 2000s, there was an increase in the amount of matter consumed within the ecosystem (from 4.8 ± 0.5 to 7.3 ± 0.9 t km^{-2} yr^{-1}). The main prey was capelin (43% of all matter consumed) followed by shrimp (22%) and planktivorous small pelagics (14%). Mackerel was generally the seventh most abundant prey

consumed within the northern Gulf during each period (nearly 3% of all matter consumed in each period).

In the southern Gulf, there was no difference in the amount of matter consumed within the ecosystem from the mid-1980s to mid-1990s (8.1 t km^{-2} yr^{-1}; Figure 6) when planktonic and benthic invertebrate groups were not considered in the calculation. However, the relative size of the compartments processing this matter changed substantially. Planktivorous small pelagics, shrimp, small American plaice, and piscivorous small pelagics (mainly mackerel) were the main prey in the southern Gulf (combined = 65% of matter consumed) during the mid-1980s (Figure 6). In contrast, capelin was the most important prey during the 1990s followed by shrimp, planktivorous small pelagics, and small American plaice (combined = 79% of matter consumed).

Main causes of mackerel mortality

In the northern Gulf, predation was the main cause of mackerel mortality during the mid-1980s (84% of total mortality; Figure 7). Other mortality causes and fishing mortality represented 14 and 2% of total mortality, respectively. Cetacea were the main predators followed by large cod and large demersals. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.22, 0.01, and 0.04 yr^{-1}, respectively (total: 0.26 yr^{-1}). From the mid-1980s to mid-1990s, there was a three-fold decrease in total mortality (from 0.64 ± 0.17 to 0.20 ± 0.02 t km^{-2} yr^{-1}; Figure 7). Predation mortality decreased from 0.54 ± 0.15 t km^{-2} yr^{-1} during the mid-1980s to 0.16 ± 0.02 t km^{-2} yr^{-1} during the mid-1990s. Predation dominated total mortality (81% of total mortality) during the mid-1990s while other mortality causes and fishing accounted for 5 and 14%, respectively. Cetacea and grey and harbour seals were the main predators of mackerel (Figure 7). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.29, 0.05, and 0.02 yr^{-1}, respectively (total: 0.36 yr^{-1}). From the mid-1990s to the early 2000s, total mortality values were similar (0.20 ± 0.02 t km^{-2} yr^{-1} vs 0.25 ± 0.03 t km^{-2} yr^{-1}; Figure 7). Predation dominated total mortality (65% of total mortality) during the early 2000s while other mortality causes and fishing accounted for 5 and 30%, respectively. Fishing mortality increased from 0.03 ± 0.00 t km^{-2} yr^{-1} for the mid-1990s to 0.07 ± 0.02 t km^{-2} yr^{-1} for the early 2000s. Cetacea and grey and harbour seals were still the main predators of mackerel (Figure 7). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.31, 0.14, and 0.02 yr^{-1}, respectively (total: 0.47 yr^{-1}).

In the southern Gulf, predation was also the main cause of mackerel mortality during the mid-1980s (66% of total mortality; Figure 8). Other mortality causes and fishing mortality represented 23 and 12% of total mortality, respectively. Large cod were the main predators followed by harp and hooded seals and cetacea. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.15, 0.03, and 0.05 yr^{-1}, respectively (total: 0.23 yr^{-1}). From the mid-1980s to mid-1990s, there was a three-fold decrease in total mortality (from 1.14 ± 0.23 to 0.44 ± 0.05 t km^{-2} yr^{-1}; Figure 8). Predation mortality decreased also by a factor of three, from 0.75 ± 0.15 t km^{-2} yr^{-1} during the mid-1980s to 0.23 ± 0.08 t km^{-2} yr^{-1} during the mid-1990s. Predation slightly dominated total mortality (51% of total mortality) during the mid-1990s while other mortality causes and fishing accounted for 15 and 33%, respectively. Cetacea were the main predators followed by grey and harbour seals and harp and hooded seals (Figure 8). In absolute terms, fishing mortality was the main mortality cause. Annual mortality rates for predation,

fishing, and other mortality causes were estimated at 0.20, 0.13, and 0.06 yr^{-1}, respectively (total: 0.38 yr^{-1}).

DISCUSSION / CONCLUSION

Biomass increases after release from cod predation have been observed in small pelagic fishes such as capelin, herring, and sprat (*Sprattus sprattus*) (Lilly 1991, Garrison and Link 2000, Köster et al. 2001). In the northern and southern Gulf ecosystems, the ecosystem structure shifted dramatically from one previously dominated by piscivorous groundfish and small-bodied forage species (i.e., capelin, mackerel, herring, and shrimp) to one now dominated by small-bodied forage species and marine mammals (Savenkoff et al. submitted a, b). Research vessel survey data revealed a major expansion in the geographical distribution of capelin throughout the Gulf of St. Lawrence in the 1990s (DFO 2001, Savenkoff et al. 2004d). This expansion is confirmed by an increase in the contribution of capelin to the diet compositions of cod (small cod: from 0.0 to 2.1%; large cod: from 2.0 to 5.5%) and mackerel (from 6.7 to 11.4%) from the mid-1980s to the mid-1990s in the southern Gulf (Savenkoff et al. 2004c). However, biomass of both piscivorous (mainly Atlantic mackerel) and planktivorous (mainly Atlantic herring and sand lance) small pelagics decreased from the mid-1980s to the early 2000s in the northern Gulf (planktivorous: from 5.42 ± 0.43 to 3.57 ± 1.90 t km^{-2}) and from the mid-1980s to mid-1990s in the southern Gulf (planktivorous: from 9.75 ± 1.82 to 7.42 ± 0.15 t km^{-2}).

In both the northern and southern Gulf ecosystems, there was a net decrease in total mortality and predation on mackerel from the mid-1980s to mid-1990s. Fishing mortality increased from the mid-1980s to early 2000s in the northern Gulf while fishing was similar among time periods in the southern Gulf. Although annual mortality rates due to predation and fishing increased with time in each ecosystem, the most noticeable increase in mortality came from fishing in the northern Gulf from the mid-1980s to early 2000s (from 0.01 to 0.14 yr^{-1}) and in the southern Gulf from the mid-1980s to mid-1990s (from 0.03 to 0.13 yr^{-1}). Increased fishing mortality may have countered the expected increase in biomass of this species following the net decrease in demersal biomass and the ensuing drop in predation. For capelin, fishing mortality does not appear to have a noticeable effect on the population at the current landing levels (at most 1% of total mortality; Savenkoff et al. 2004d).

The Gulf of St. Lawrence experienced below-normal water temperatures in the cold intermediate layer between 1986 and 1998 (DFO 2004). Between 1985 and 2002, the annual mackerel condition (Fulton) was below the average value for the 1973–2002 period (except in 1999) (DFO 2003). The annual variations in mackerel condition follow a pattern very similar to water temperature in the cold intermediate layer (30-100 m). The possible relationship between mackerel condition and temperature is not well known, but it is assumed that a decline in condition like that observed in the 1980s and 1990s may have had a negative impact on the natural mortality of mackerel (DFO 2003). Supporting the idea of an adverse effect of cold temperatures on survival, poor condition (energy reserves) has been documented in the northern Gulf cod between the mid-1980s and the mid-1990s (Lambert and Dutil 1997, Dutil and Lambert 2000, Dutil et al. 2003).

In our models, however, fishing mortality may have been underestimated: we have reliable evidence for non-negligible misreporting (non-reported landings and discards at sea). A

disturbing observation was made during the fall of 2004 in the southern Gulf of St. Lawrence concerning the discards of small mackerel whose length was under the minimum allowable catch size or below what industry requires (DFO 2005). This may explain what may have occurred during modelled periods. These discards, which were from line fisheries, caused mortalities that are difficult to calculate. Nevertheless, they were certainly significant given the fact that this type of fishery is predominant in the southern Gulf during the fall. Also, recreational catches and those made by bait fishermen are not recorded and also could increase fishing mortality (DFO 2005). Recreational catches are a significant part of the overall picture, considering that this fishing is carried out by a large number of fishermen, including tourists, all along the Atlantic coast (DFO 2005). In our models, total mortality was equal to production. Production estimates were close to the maximum production constraints in the northern Gulf for each period, while they were close to the mean production in the southern Gulf (i.e., production and thus total mortality could be higher) (Table 3). All these findings seem to target the southern Gulf ecosystem as a place where unaccounted fishing mortality may have occurred.

Monitoring programs (fishery statistics, commercial sampling, and research surveys) allow a fair assessment of the past and current status of the stocks. However, recurrent information on the impact of fishing and predation on the Atlantic mackerel stock in the Gulf of St. Lawrence has to be investigated to improve management practices. The successful development of ecosystem models will provide powerful new tools for fishery management. The model solutions could be used as baselines (knowledge integration) for the development of ecosystem-based management plans. The results already provide valuable information on the impact of fishing effort and catch rates of exploited species of these ecosystems and on the effects of the major mortality causes (fishing, predation, and natural mortality other than predation) on the fish and invertebrate communities.

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Table 1. Functional groups used in modelling in the northern and southern Gulf of St. Lawrence for each time period.

Group name	Main species
Cetaceans[a]	Mysticeti or baleen whales: *Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Megaptera novaeangliae*
	Odontoceti or toothed whales: *Lagenorhynchus acutus*, *L. albirostris*, *Phocoena phocoena*
Harp seals[b]	*Pagophilus groenlandica*
Hooded seals[b]	*Cystophora cristata*
Grey seals[c]	*Halichoerus grypus*
Harbour seals[c]	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *P. auritus*, *Larus delwarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)[d]	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)[d]	*Reinhardtius hippoglossoides*
Large American plaice (> 35 cm)[e]	*Hippoglossoides platessoides*
Small American plaice (≤ 35 cm)[e]	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *Sebastes fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinus*, *Centroscyllium fabricii*, *Anarhichas* spp., *Cyclopterus lumpus*, *Lycodes* spp., Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalus* spp., *Tautogolabrus adspersus*, *Macrozoarces americanus*, juvenile large demersals
Capelin	*Mallotus villosus*
Sand lance[f]	*Ammodytes* spp.
Arctic cod[g]	*Boreogadus saida*

Table 1. Cont.

Group name	Main species
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*
Piscivorous small pelagic feeders	*Scomber scombrus*, piscivorous myctophids and other mesopelagics, *Illex illecebrosus*, piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	*Clupea harengus*, planktivorous myctophids and other mesopelagics, *Scomberesox saurus*, *Gonatus* spp., planktivorous juvenile large pelagics
Shrimp[h]	*Pandalus borealis*, *P. montagui*, *Argis dentata*, *Eualus macilentus*, *E. gaimardii*
Crabs[i]	*Chionoecetes opilio*, other non-commercial species (e.g., *Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Strongylocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Exogone hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)

Table 1. Cont.

Group name	Main species
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *C.* spp., *Leptocylindrus minimus*, *Thalassiosira nordenskioeldii*, *T.* spp., *Fragilariopsis* spp., and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, and Prymnesiophytes
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

[a]: Cetaceans were separated into two groups for the early 2000s in the northern Gulf model: the mysticeti (baleen whales) and the odontoceti (toothed whales).
[b]: Harp and hooded seals were grouped for the northern Gulf model in the early 2000s.
[c]: Grey and harbour seals were grouped for the northern Gulf model in the early 2000s.
[d]: Aggregated as Greenland halibut for the southern Gulf models.
[e]: Aggregated as American plaice for the northern Gulf models.
[f]: Included in the planktivorous small pelagic feeders for the southern Gulf models and for the northern Gulf model in the early 2000s.
[g]: Included in the capelin group for the southern Gulf models and for the northern Gulf model in the early 2000s.
[h]: shrimp were separated into large shrimp, mainly females (≥ 22 mm CL; mainly *Pandalus borealis* species), and small shrimp (< 22 mm CL) for the northern Gulf model in the early 2000s.
[i]: crabs were separated into small (≤ 45 mm CW) and large (> 45 mm CW) crabs for the northern Gulf model in the early 2000s.

Table 2. Annual mackerel landings (t) by NAFO area since 1995. -: no data.

Division and region	Year										Average
	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004[a]	(1995–2003)
3K	11	3	0	0	0	0	322	6566	588	11511	832
3L	6	0	0	0	0	0	10	3	0	37	2
3P	86	60	8	65	7	19	102	135	105	-	65
4R	2760	3767	1181	2175	1438	2001	8385	11251	25938	21418	6544
4S	30	9	1	1	2	0	17	2	0	0	7
4T	8184	11355	15358	12739	10562	7005	11915	14251	14106	2057	11719
4V	1475	1591	838	554	762	576	125	308	60	-	699
4W	621	1181	716	138	127	120	248	115	9	-	364
4X	4478	2399	3208	3662	3663	3663	2743	1771	3669	-	3251
Scotian Shelf (4VWX)	6574	5170	4762	4355	4552	4358	3117	2194	3737	-	4313
Gulf of St. Lawrence (4RST)	10973	15131	16540	14914	12002	9006	20317	25504	40044	23475	18270
East and south coasts of Newfoundland (3KPL)	103	63	8	65	7	19	434	6704	693	11548	900
Total	17650	20364	21309	19334	16561	13383	23868	34402	44475	35023	23483

[a]Preliminary

Table 3. Observed biomass, lower and upper modelling constraints, and estimated fluxes for mackerel made using inverse modelling for each ecosystem and each time period.

Parameter	Northern Gulf			Southern Gulf	
	Mid-1980s	Mid-1990s	Early 2000s	Mid-1980s	Mid-1990s
Observed mean biomass (t km^{-2})	2.46	0.56	0.52	4.93	1.16
Observed minimum biomass (t km^{-2})	1.67	0.24	0.32	3.36	0.52
Observed maximum biomass (t km^{-2})	3.36	0.88	0.73	6.74	1.79
Observed mean production (t km^{-2} yr^{-1})	0.48	0.14	0.17	1.09	0.40
Constrained minimum production (t km^{-2} yr^{-1})	0.34	0.08	0.08	0.75	0.28
Constrained maximum production (t km^{-2} yr^{-1})	0.68	0.20	0.25	1.54	0.53
Estimated production (t km^{-2} yr^{-1})	0.64	0.20	0.25	1.14	0.44
Observed mean consumption (t km^{-2} yr^{-1})	8.63	2.21	1.88	17.29	4.52
Constrained minimum consumption (t km^{-2} yr^{-1})	2.46	0.56	0.56	4.93	1.16
Constrained maximum consumption (t km^{-2} yr^{-1})	14.79	3.85	3.21	29.65	7.88
Estimated consumption (t km^{-2} yr^{-1})	2.71	0.93	1.09	8.01	3.36
Observed mean catch (t km^{-2} yr^{-1})	0.012	0.029	0.068	0.142	0.144
Constrained minimum catch (t km^{-2} yr^{-1})	0.002	0.025	0.018	0.112	0.118
Constrained maximum catch (t km^{-2} yr^{-1})	0.032	0.037	0.108	0.186	0.164
Estimated catch (t km^{-2} yr^{-1})	0.013	0.028	0.074	0.133	0.147

Table 4. Diet compositions of mackerel used in modelling of the northern Gulf for each time period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	1985–1987					1994–1996					2000–2002				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Small cod	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Greenland halibut															
American plaice											**0.0**	0.0	0.0	0.0	0.0
Flounders											**0.0**	0.0	0.0	0.0	0.0
Skates															
Redfish															
Large demersals															
Small demersals	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0	**0.1**	0.2	0.0	0.2	0.1
Capelin	**0.0**	0.0	0.0	0.0	0.0	13.2	21.6	**0.0**	**30.6**	16.2	8.4	21.9	**0.0**	**31.0**	13.5
Large pelagics															
Pisci. small pelagics											0.1	0.4	**0.0**	**0.5**	0.1
Plank. small pelagics	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0	12.4	32.1	**0.0**	**45.4**	1.8
Shrimp	**0.2**	0.3	0.0	0.4	0.2	**0.2**	0.3	0.0	0.4	0.2	21.9	40.3	**0.0**	**80.6**	3.6
Crabs															
Echinoderms															
Molluscs	**0.2**	0.3	0.0	0.4	0.2	**0.2**	0.3	0.0	0.4	0.2	**0.1**	0.3	0.0	0.4	0.1
Polychaetes															
Other bent. inver.											2.6	6.8	**0.0**	**9.7**	5.3
Large zooplankton	54.2	64.1	**8.9**	**99.6**	22.1	47.0	64.1	**8.9**	**99.6**	38.7	27.1	70.4	**0.0**	**99.6**	24.0
Small zooplankton	45.5	64.4	**0.0**	**91.1**	77.5	39.4	64.4	**0.0**	**91.1**	44.8	27.2	70.7	**0.0**	**100.0**	51.5
Phytoplankton															
Detritus															
Total	100.0		8.9	191.4	100.0	100.0		8.9	222.0	100.0	100.0		0.0	367.4	100.0
TRN	8					8					12				

Table 5. Diet compositions of mackerel used in modelling of the southern Gulf for each time period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	1985–1987					1994–1996				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Small cod										
Greenland halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin	6.7	8.0	**0.0**	**11.4**	0.0	11.4	16.0	**0.0**	**22.7**	18.8
Large pelagics										
Pisci. small pelagics	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Plank. small pelagics	5.3	6.3	**0.0**	**8.9**	5.4	8.9	32.1	**0.0**	**45.4**	5.0
Shrimp	5.1	6.1	**0.0**	**8.6**	0.0	**8.6**	57.0	0.0	80.6	8.6
Crabs										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	**0.4**	0.4	0.0	0.6	0.4	**0.6**	6.8	0.0	9.7	0.6
Large zooplankton	24.2	17.0	**14.3**	**38.4**	34.1	14.3	52.8	**0.0**	**74.6**	19.7
Small zooplankton	58.4	3.8	**56.2**	**61.6**	60.0	56.2	68.3	**3.4**	**100.0**	47.3
Phytoplankton										
Detritus										
Total	100.0		70.5	129.5	100.0	100.0		3.4	333.0	100.0
TRN	7					7				

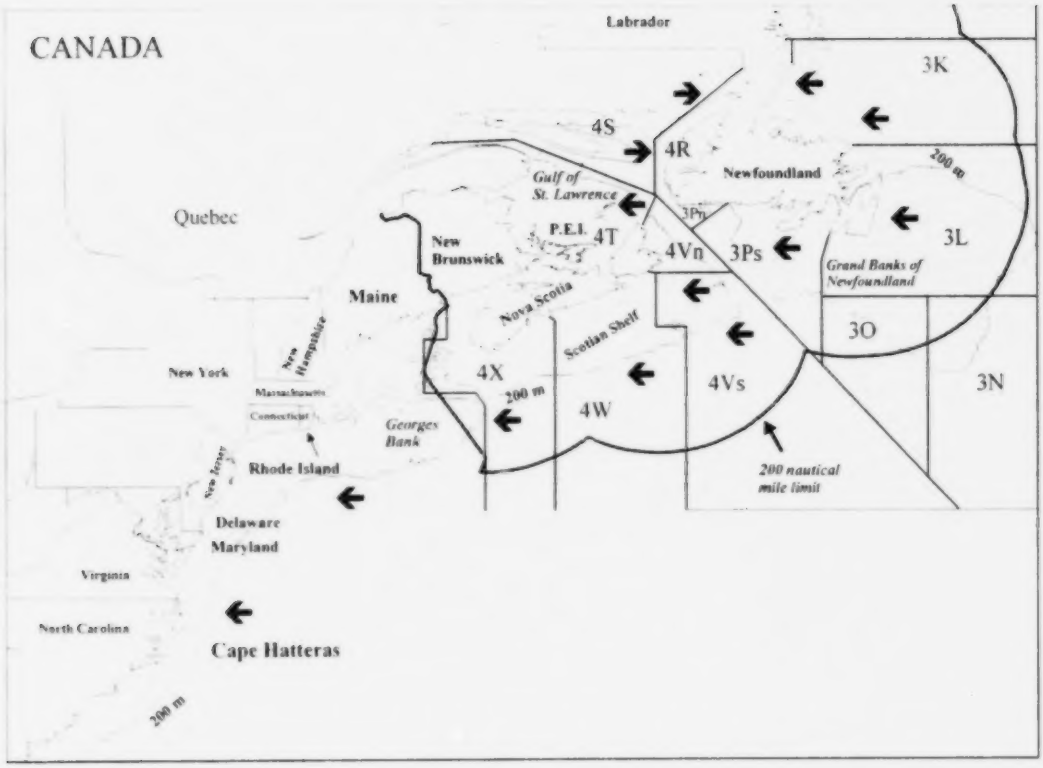

Figure 1. Distribution (←) of Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic.

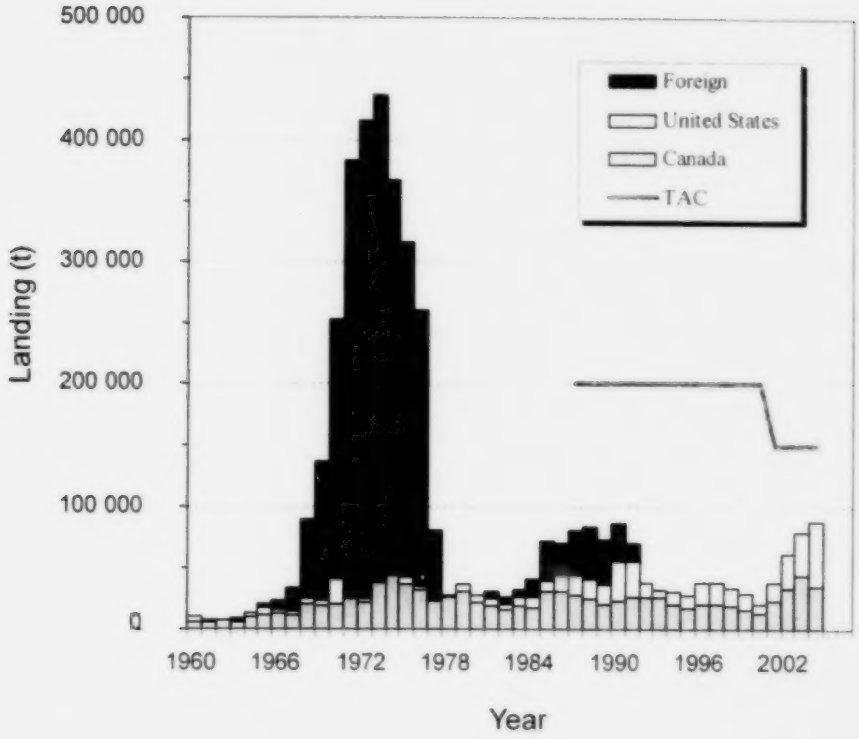

Figure 2. Total mackerel landings and total allowable catch (TAC, t) for the Northwest Atlantic since 1960.

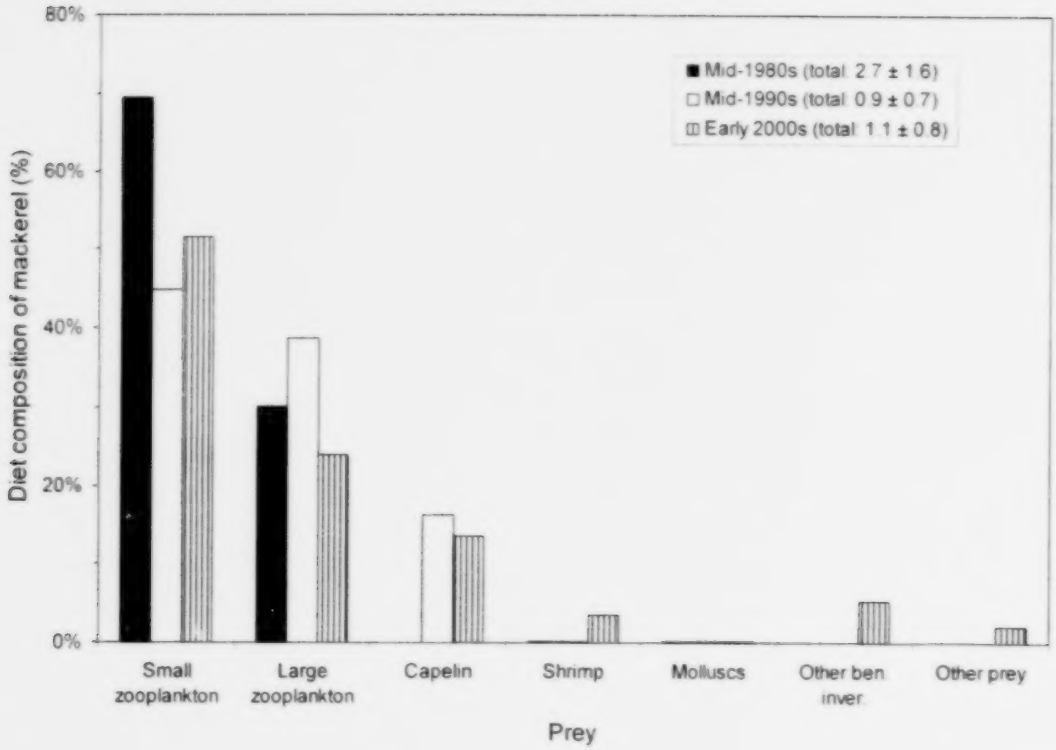

Figure 3. Diet composition of mackerel estimated for each time period in the northern Gulf. Total mackerel consumption for each time period (in t km^{-2} yr^{-1}) is shown in the legend.

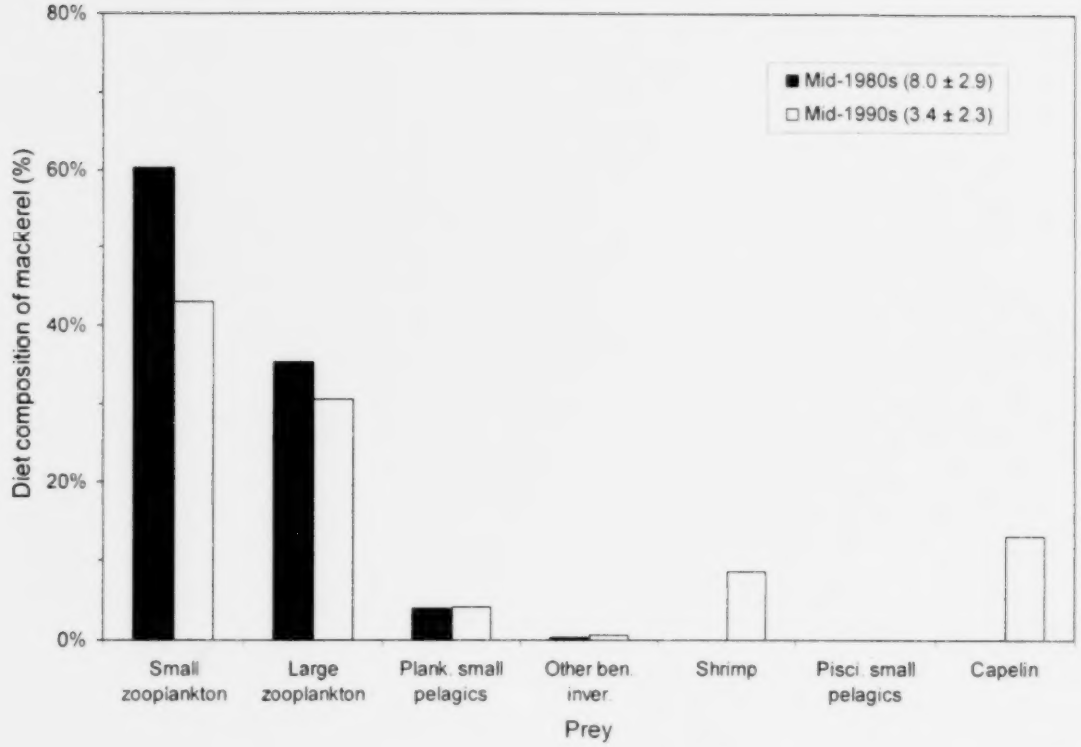

Figure 4. Diet composition of mackerel estimated for each time period in the southern Gulf. Total mackerel consumption for each time period (in t km^{-2} yr^{-1}) is shown in the legend.

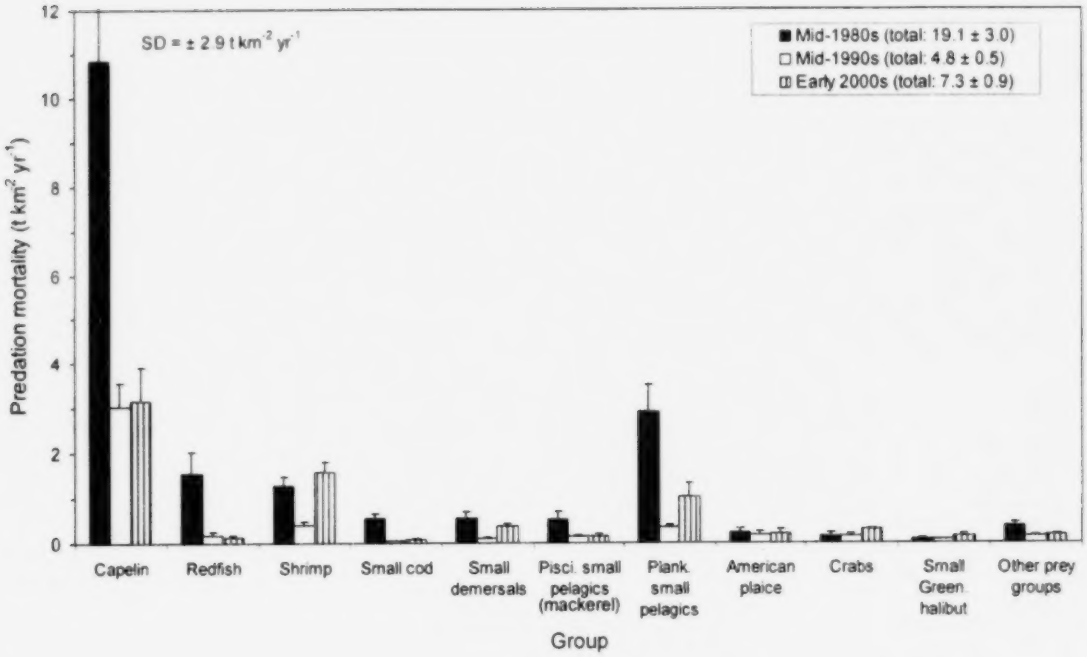

Figure 5. Main vertebrate and crustacean prey consumed in the northern Gulf estimated for each time period. Bars show mean values and SD.

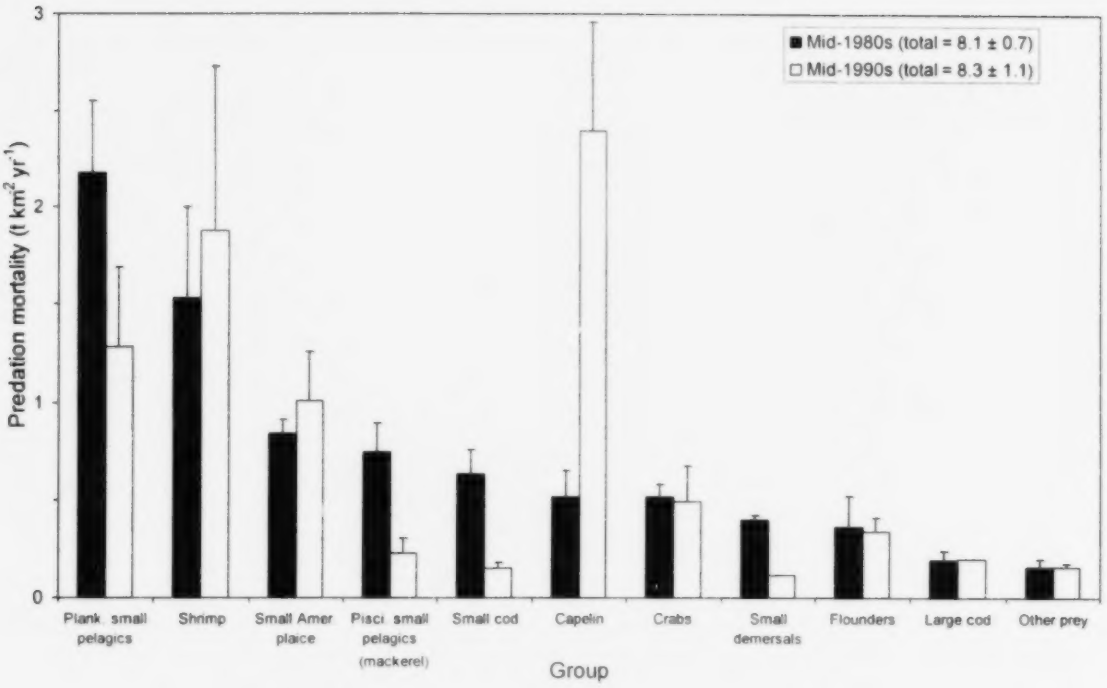

Figure 6. Main vertebrate and crustacean prey consumed in the southern Gulf estimated for each time period. Bars show mean values and SD.

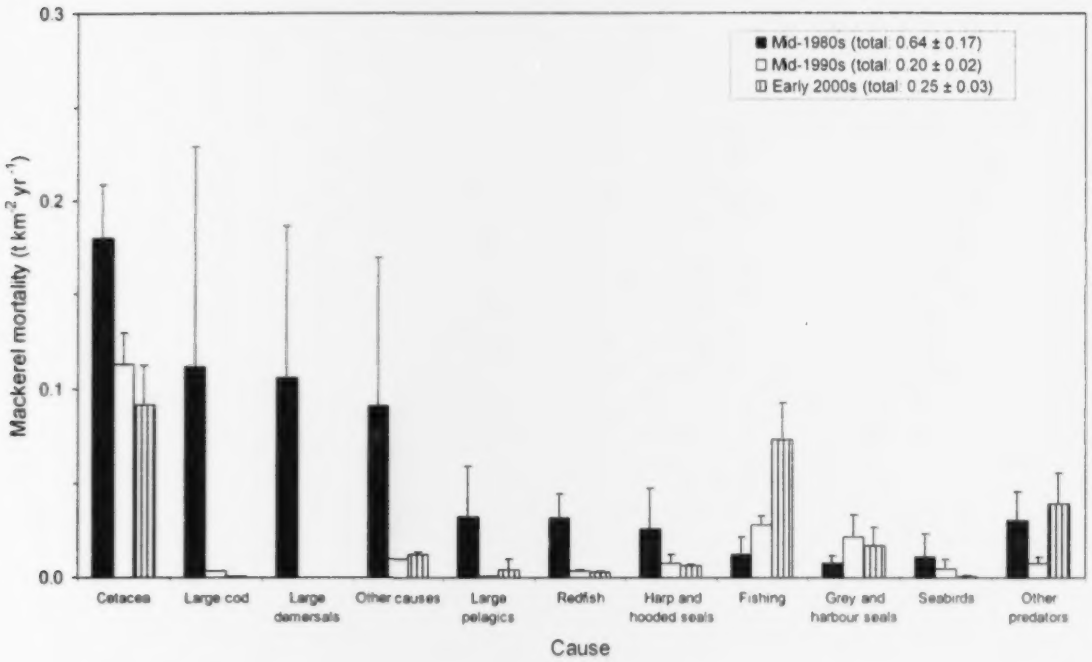

Figure 7. Main causes of mackerel mortality (fishing, predation, and natural mortality other than predation, i.e., other causes) estimated for each time period in the northern Gulf. Bars show mean values and SD.

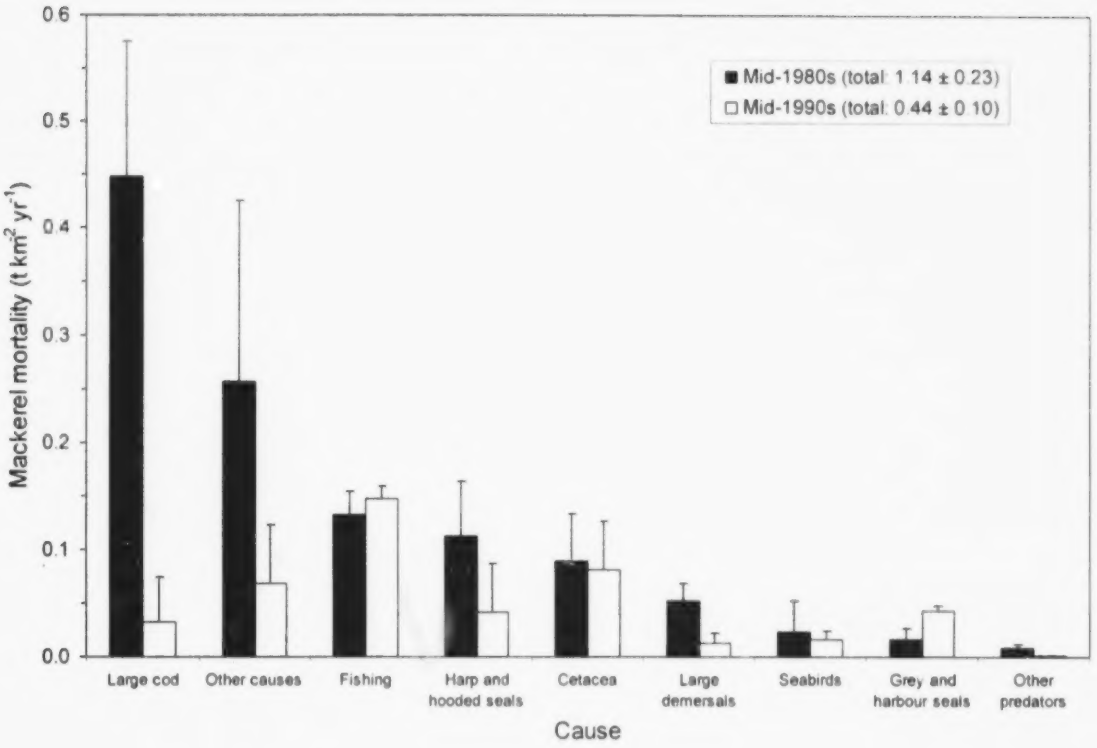

Figure 8. Main causes of mackerel mortality (fishing, predation, and natural mortality other than predation, i.e., other causes) estimated for each time period in the southern Gulf. Bars show mean values and SD.